A Basal Actinopterygian Fish from the Middle Devonian Bunga Beds of New South Wales, Australia.

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A partial articulated skeleton of a basal actinopterygian fish is described from the Middle Devonian Bunga Beds of New South Wales. The specimen represents a new species and is questionably assigned as a congener of *Howqualepis rostridens* from the Middle Devonian of central Victoria. This represents the first record of an articulated postrcranium of a Devonian ray-finned fish from New South Wales. The pectoral fin of *Howqualepis* is also redescribed based on a re-examination of Victorian material. The fin is broader in shape and less extensively unsegmented than previously recognised. The close similarity of the new form with contemporaneous taxa from Victoria and the Aztec Siltstone of Antarctica adds to an already wide body of evidence supporting a regionally endemic freshwater vertebrate fauna in the Middle Devonian of Eastern Gondwana.

Manuscript received 7 Feb 2008, accepted for publication 22 October 2008.

KEYWORDS = Actinopterygians, Bunga Beds, Devonian, fish, Howqualepis, New South Wales

INTRODUCTION

In stark contrast to their modern abundance and diversity, actinopterygians are a sparse component of most Devonian vertebrate assemblages. Australia is notable in producing some of the finest fossils of Devonian actinopterygians, the best known of which are exceptionally preserved specimens from the Frasnian Gogo Formation of northern Western Australia. Included within the assemblage are *Moythomasia durgaringa* (Gardiner & Bartram 1977, Gardiner 1984), the currently preoccupied "*Mimia*" *toombsi* (ibid), *Gogosardina coatesi* (Choo et. al, in press) and at least two additional forms (Choo, in prep).

Southeastern Australian fossil sites have also produced a substantial amount of early ray-finned fishes. The first record of Australian Devonian actinopterygians consisted of the isolated scales of *Ligulalepis toombsi* from the Lower Devonian Taemas-Wee Jasper Limestones of New South Wales (Schultze 1968). A subsequently discovered braincase and skull-roof was assigned to this genus (Basden *et al.* 2000, Basden & Young 2001). Long (1988) described *Howqualepis rostridens* based on numerous specimens from the Givetian Mt Howitt fauna of central Victoria (age revised in Young, 1999).

Adding to this Eastern Australian record is an incomplete but articulated fossil that was recently discovered by Gavin Young from the Middle Devonian Bunga Beds, near the shoreline at Bunga Beach in south coastal New South Wales. This represents the first discovery of an articulated Devonian actinopterygian postcranium from New South Wales. Subsequent repeated searches failed to recover additional material of this form (Gavin Young, pers. com.).

GEOLOGICAL SETTING

The Bunga Beds represent a thinly bedded sequence of carbonaceous shale and sandstone that comprises the lowest section of an extensively fossiliferous Devonian sequence (Fergusson et al. 1979, Young 2007). Young (2007, figs 1, 2) provides and up to date account of the lithology, fossil assemblage and possible age of the Bunga Beds. The age of the unit is poorly constrained and probably older than the Late Devonian age stated in recent

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The dark shales of the Bunga Beds are highly fossiliferous with abundant plant material and uncommon vertebrate remains (Young 2007, fig. 3), possibly representing a deepwater lacustrine depositional environment. The fossil fish fauna includes ischnacanthid acanthodians (Burrow 1996), several taxa of chondrichthyans including *Antarctilamna prisca* (Young 1982), originally described from the Givetian Aztec Silstone of Antarctica, and a possible tetrapodomorph sarcopterygian (Young 2007, table 1). The fossil ichthyofauna of the Bunga Beds seems impoverished due to the apparent absence of placoderms and dipnoans that are abundant in other southeastern Australian sites of a similar age.

MATERIALS AND METHODS

The fossil was recovered as a natural mould set within a matrix of dark shale. After collection, the specimen was split into part and counterpart and bone remnants removed. Bone margins were exposed with mechanical preparation and the impressions of the fish were examined using a latex rubber cast whitened with ammonium chloride. For comparison, fresh latex casts were made from the following specimens of *Howqualepis rostridens* in Museum Victoria (MV) = P.160745A, P.160782A, P.160788, P.160792B, P.160811, P.160822A, P.160851B, P.160857.

Abbreviations for actinpterygian dermal bones and other structures used in the text and figures are as follows: **an.f**, anal fin; **Br. 1**, 1st branchiostegal ray; **Br. 7**, 7th branchiostegal ray; **c.ful**, caudal (basal) fulcra; **Clav**, clavicle; **Clth**, cleithrum; **cw.lep**, cutwater of short lepidotrichial segments; **d.lep**, probable dorsal lepidotrichia; **f.ful**, fringing fulcra; **nm**, notochordal mass of caudal fin; **Op**, operculum; **Sop**, suboperculum; **pec.f**, pectoral fin; **pel.f**, pelvic fin; **pseg**, segmented posterior lepidotrichia on pectoral fin; **tfr**, terminal fringe of fine branching segments on pectoral fin; **vhl**, ventral hypochordal lobe of caudal fin; **useg**. unsegmented proximal lepidotrichia on pectoral fin.

SYSTEMATIC PALAEONTOLOGY

CLASS OSTEICHTHYES Huxley, 1880 SUBCLASS ACTINOPTERYGII, Cope, 1887 Family Howqualepididae Long, Choo and Young, 2008

Diagnosis (revised)

Basal actinopterygians with an open spiracular slit bordered by the intertemporal, dermosphenotic and supratemporal. Intertemporal is very small (less than 1/3 the size of parietals). Pineal foramen present on anterior half of the median frontal contact. Dermosphenotic is elongate and tripartite. Suboperculum has a prominent anterodorsal process. Body form is elongate and fusiform. Squamation macromeric; scales are rhombic with linear ganoine ornamentation. Fringing fulcra are spine-like terminal sections of the anterior fin rays, lacking median contact between the hemilepidotrichia. Longest anterior pectoral fin rays are proximally unsegmented for over 60% of their length. Median scute series on dorsal and ventral surface do not extend anteriorly to reach the head.

Remarks

Diagnosis slightly modified from Long et. al (2008) to incorporate the revised description of the pectoral fin and fringing fulcra of *Howqualepis* presented below.

Genus ?Howqualepis Long, 1988 ?Howqualepis youngorum sp. nov.

Etymology

After Professor Gavin Young (ANU) who discovered the holotype specimen and Mr Ben Young for conducting both the preparatory work as well as the key photography of the specimen.

Repository

The type and only known specimen is lodged in the collections of the Department of Earth & Marine Sciences, Australian National University, Canberra, represented in the text by the prefix **ANU V**.

Holotype.

ANU V2929a, b, an incomplete, partially articulated fish preserved laterally in part and counterpart. Consists of an incomplete operculargular series, cleithrum, clavicle, scales and all fins except the dorsal fin (Figs. 1-4). Collected by Gavin Young (ANU) from the Bunga Beds at Bunga Beach, south of Bermagui, New South Wales.

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A *Howqualepis* with more than 54 primary lepidotrichia on the anal fin and porous ornamentation on the cleithrum and clavicle.

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Diagnosis

A *Howqualepis* with more than 54 primary lepidotrichia on the anal fin and porous ornamentation on the cleithrum and clavicle.

Remarks

Tentatively assigned to the genus Howqualepis. The extensive unsegmented pectoral lepidotrichia of ?Howqualepis youngorum sp.nov separates this taxon from all other Devonian actinopterygians Howqualepis rostridens Long, 1988. except Donnrosenia schaefferi Long, Choo and Young, 2008, and Tegeolepis clarki Newberry, 1888. ?H. youngorum differs from Donnrosenia in that the unsegmented fin-rays account for more than 75% of the total length of the pectoral fin. ?H. youngorum differs from Tegeolepis in possessing macromeric squamation, long-based pelvic fins and a segmented terminal fringe on the pectoral fin. Separable from H. rostridens in having porous (as opposed to entirely linear) ornament on the pectoral girdle and in having a larger anal fin (54+ vs 45 primary lepidotrichia).

DESCRIPTION

Overall body form

ANU V2929 is preserved in lateral aspect (Fig. 1). The anterior part of the specimen terminates at

an oblique breakage margin, with elements of the opercular-gular series and pectoral girdle preserved along with the pectoral fin (Fig. 2). 2.5 cm behind this is an incomplete pelvic fin with patches of squamation present above and to the rear of the fin (Fig. 3). The largest preserved segment comprises the rear section of the fish, including well preserved anal and caudal fins along with extensive squamation (Fig. 4). The preserved sections suggest a highly elongate, fusiform body form similar to that of *Howqualepis rostridens* (Long 1988) and quite unlike the more compact and robust form of "*Mimia*" or *Moythomasia* (Jessen 1968, Gardiner 1984).

As preserved, the fossil measures slightly less than 12 cm from the anterior preserved edge of the clavicle to the posteriormost caudal scales. Assuming that the missing portions of the fish were of similarly proportions to that of *Howqualepis rostridens*, the complete fish would have measured about 14 cm from snout to caudal peduncle.

Opercular-gular series

A section of the dermal operculo-gular series of ANU V2929 is preserved in articulation and comprises

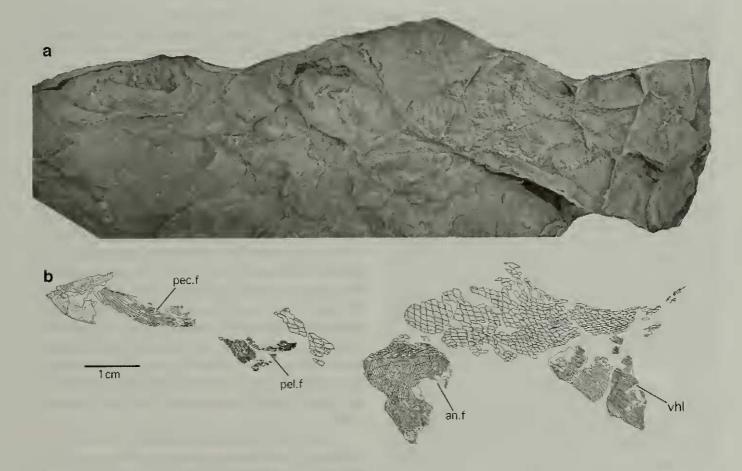


Figure 1. *?Howqualepis youngorum* sp. nov. a. photograph and b. line drawing of holotype (ANU V2929A) showing the entire preserved fossil in lateral view. The specimen is a latex cast whitened with ammonium chloride.

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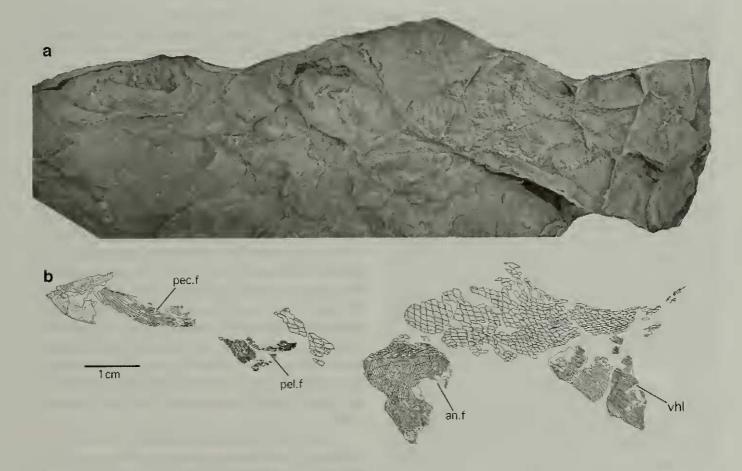


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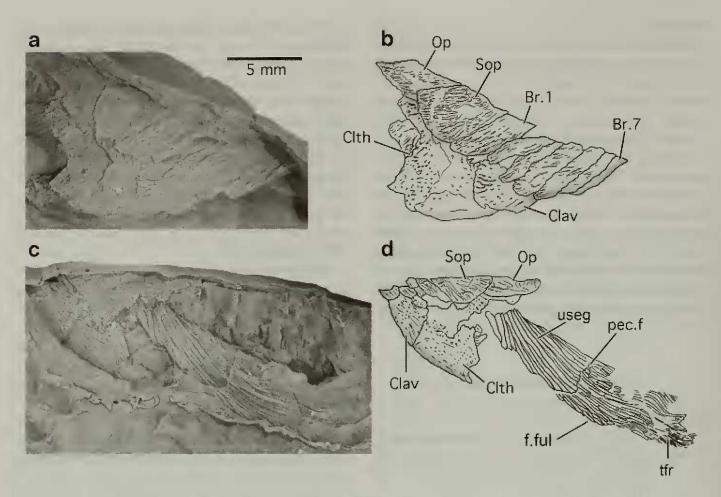


Figure 2. *?Howqualepis youngorum* sp. nov. a. photograph and b. line drawing of the pectoral girdle and opercular-gular series of the holotype counterpart (ANU V2929B), c. photograph and d. line drawing of pectoral girdle, opercular-gular series and pectoral fin of the holotype (ANU V2929A).

a posteroventral fragment of the operculum, a partial suboperculum, and at least seven branchiostegal rays (Fig.2). The anterior portions of most of these elements are missing, the preserved sections terminating at a margin of clean breakage, suggesting that a substantial portion of the fossil, possibly including the skull, was lost prior to collection due to weathering.

The posterodorsal-most bone in the series is tentatively identified as the posterovental fragment of an operculum. It is an oblong bone bone, missing the dorsal and anterior margins. The bone surface is ornamented with short, posterolaterally directed linear ridges. The suboperculum is rectangular with a convex posterior margin. Ornament consists of short linear ridges that extend to near the posterior bone margin.

At least seven branchiostegal rays are visible on ANU V2929b (Fig. 2). The first branchiostegal ray, whose dorsal margin is overlapped by the suboperculum, is more than twice as thick dorsoventrally as the other bones in the series. The 2nd ray is poorly preserved while the 3rd is narrower than the following two rays. Rays 6 and 7 are very narrow. Ornament on all bones in this series consists of short rostrocaudally directed ridges with little evidence of the tubercular ornament present on the laterally facing branchiostegals of *Howqualepis rostridens* (Long 1988).

Pectoral girdle

A partial cleithrum and clavicle (Fig. 2) have a similar overall shape to those of most early actinopterygians. The cleithrum consists of an expanded ventral region with a slender vertically directed blade although the dorsal portion of this structure is missing. The bone is convex postiorly with a moderately deep embayment on the posterior margin for the insertion of the pectoral fin, similar to that of *H. rostridens* (Long 1988. Fig.27). The clavicle is triangular and overlaps the cleithrum posteriorly and is itself dorsally overlapped by the branchiostegal rays.

Preserved sections of ornament on both the cleithrum and clavicle consists of limited areas of short ridges, particularly around the posterior margin of the clavicle and the vertical blade of the cleithrum, that are largely replaced by rostrocaudally oriented

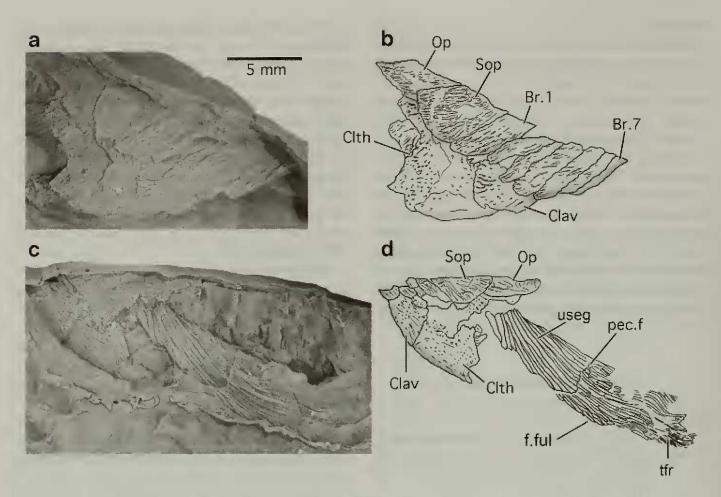


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Preserved sections of ornament on both the cleithrum and clavicle consists of limited areas of short ridges, particularly around the posterior margin of the clavicle and the vertical blade of the cleithrum, that are largely replaced by rostrocaudally oriented rows of small pores over most of the remainder of the bone surface. This differs from the condition in *Howqualepis rostridens* where the dermal surface of the corresponding area is covered in a mixture of ridges and raised tubercles with no porous ornamentation (Long, 1988. Fig.15). *Donnrosenia* has very similar ornamentation on the clavicle but has entirely linear ornamentation on the cleithrum (Long, Choo & Young, 2008. Fig.6). *Moythomasia durgaringa* and *M. nitida* also have porous ornamentation on the pectoral girdle, but restricted to the ventral faces of the cleithrum and clavicle (Choo, in prep) whereas pores are also present on the lateral surface in ?*H. youngorum*.

Fins

The pectoral fin (Fig. 2) is incomplete with no traces of the endoskeletal radial although the visible lepidotrichia are well preserved. The fin is elongate and triangular with more than 14 primary lepidotrichia present. As with H. rostridens and Donnrosenia, the anterior lepidotrichia are unsegmented for most of their length with secondary division restricted to the region near the fin margin. The trailing edge of the fin is not preserved and it is unclear if the posterior fin rays were fully segmented as in H. rostridens (see below). The fin reaches its maximum length at about the seventh primary ray, which is unsegmented for more than 75% of its length as in *H. rostridens*, longer than the c.65% unsegmented region in the fin of Donnrosenia (Long et.al, 2008). A short section of the leading edge is preserved with spine-like fringing fulcra formed by terminal branching of the leading fin rays. As with H. rostridens and Donnrosenia (see below) there is no medial contact visible between the distal hemilepidotrichia of each fringing fulcra on any of the fins.

The pelvic fin (Fig. 3) is long-based and triangular. Its preserved lateral aspect and does not appear to be as elongate as in *H. rostridens* although it is unclear if a section of the posterior margin is missing. The fins are located approximately midway along the body between the pectoral and anal fins. Primary lepidotrichia are only preserved for the anterior half of the fin, comprising more than 22 rays suggesting more the 40 primary rays on the entire preserved section. These rays are evenly segmented along their preserved length. Slender spine-like fringing fulcra are present on the leading edge.

The anal fin (Fig. 4a, b) is large and triangular in shape. At least 54 primary segmented lepidotrichia are present as opposed to c.45 fin rays on the anal fin of *H. rostridens*. It is unclear if the fin originally had a short posterior fringe trailing behind the main

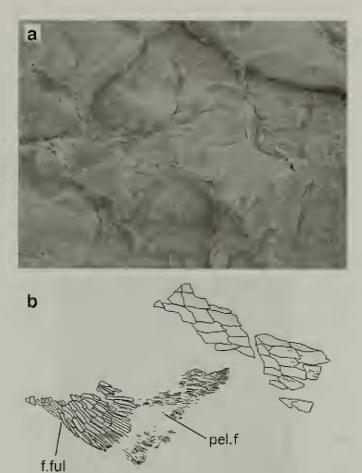


Figure 3. *?Howqualepis youngorum* sp. nov. a. photograph and b. line drawing of the pelvic fin and associated squamation on ANU V2929A.

triangular area of the fin as in *H. rostridens*. If this was the case then the complete fin would have probably had over 60 primary lepidotrichia. As in the other fins, shortened spine-like lepidotrichial segments form a serrated cutwater of fringing fulcra on the leading edge.

As was the case in other known Devonian actinopterygians, the caudal fin (Fig. 4) was heterocercal in structure with a distinct posterior cleft separating the dorsal lobe (notochordal mass of the fin plus the dorsal hypochordal lobe) from the ventral hypochordal lobe. While little of its dorsal counterpart has been preserved, the ventral hypochordal lobe is elongate and triangular with c.40 primary lepidotrichia preserved. Spine-like fringing fulcra are present on the leading edge.

The dorsal fin is not preserved in the holotype although a pair or large, isolated lepidotrichs preserved near the counterpart tail may have originated from that fin (Fig. 4d).

Scales and squamation

Articulated macromeric scales, scutes and basal fulcra are preserved from the caudal fin, extending

rows of small pores over most of the remainder of the bone surface. This differs from the condition in *Howqualepis rostridens* where the dermal surface of the corresponding area is covered in a mixture of ridges and raised tubercles with no porous ornamentation (Long, 1988. Fig.15). *Donnrosenia* has very similar ornamentation on the clavicle but has entirely linear ornamentation on the cleithrum (Long, Choo & Young, 2008. Fig.6). *Moythomasia durgaringa* and *M. nitida* also have porous ornamentation on the pectoral girdle, but restricted to the ventral faces of the cleithrum and clavicle (Choo, in prep) whereas pores are also present on the lateral surface in ?*H. youngorum*.

Fins

The pectoral fin (Fig. 2) is incomplete with no traces of the endoskeletal radial although the visible lepidotrichia are well preserved. The fin is elongate and triangular with more than 14 primary lepidotrichia present. As with H. rostridens and Donnrosenia, the anterior lepidotrichia are unsegmented for most of their length with secondary division restricted to the region near the fin margin. The trailing edge of the fin is not preserved and it is unclear if the posterior fin rays were fully segmented as in H. rostridens (see below). The fin reaches its maximum length at about the seventh primary ray, which is unsegmented for more than 75% of its length as in *H. rostridens*, longer than the c.65% unsegmented region in the fin of Donnrosenia (Long et.al, 2008). A short section of the leading edge is preserved with spine-like fringing fulcra formed by terminal branching of the leading fin rays. As with H. rostridens and Donnrosenia (see below) there is no medial contact visible between the distal hemilepidotrichia of each fringing fulcra on any of the fins.

The pelvic fin (Fig. 3) is long-based and triangular. Its preserved lateral aspect and does not appear to be as elongate as in *H. rostridens* although it is unclear if a section of the posterior margin is missing. The fins are located approximately midway along the body between the pectoral and anal fins. Primary lepidotrichia are only preserved for the anterior half of the fin, comprising more than 22 rays suggesting more the 40 primary rays on the entire preserved section. These rays are evenly segmented along their preserved length. Slender spine-like fringing fulcra are present on the leading edge.

The anal fin (Fig. 4a, b) is large and triangular in shape. At least 54 primary segmented lepidotrichia are present as opposed to c.45 fin rays on the anal fin of *H. rostridens*. It is unclear if the fin originally had a short posterior fringe trailing behind the main

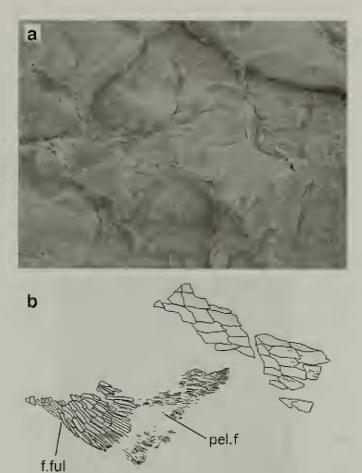


Figure 3. *?Howqualepis youngorum* sp. nov. a. photograph and b. line drawing of the pelvic fin and associated squamation on ANU V2929A.

triangular area of the fin as in *H. rostridens*. If this was the case then the complete fin would have probably had over 60 primary lepidotrichia. As in the other fins, shortened spine-like lepidotrichial segments form a serrated cutwater of fringing fulcra on the leading edge.

As was the case in other known Devonian actinopterygians, the caudal fin (Fig. 4) was heterocercal in structure with a distinct posterior cleft separating the dorsal lobe (notochordal mass of the fin plus the dorsal hypochordal lobe) from the ventral hypochordal lobe. While little of its dorsal counterpart has been preserved, the ventral hypochordal lobe is elongate and triangular with c.40 primary lepidotrichia preserved. Spine-like fringing fulcra are present on the leading edge.

The dorsal fin is not preserved in the holotype although a pair or large, isolated lepidotrichs preserved near the counterpart tail may have originated from that fin (Fig. 4d).

Scales and squamation

Articulated macromeric scales, scutes and basal fulcra are preserved from the caudal fin, extending

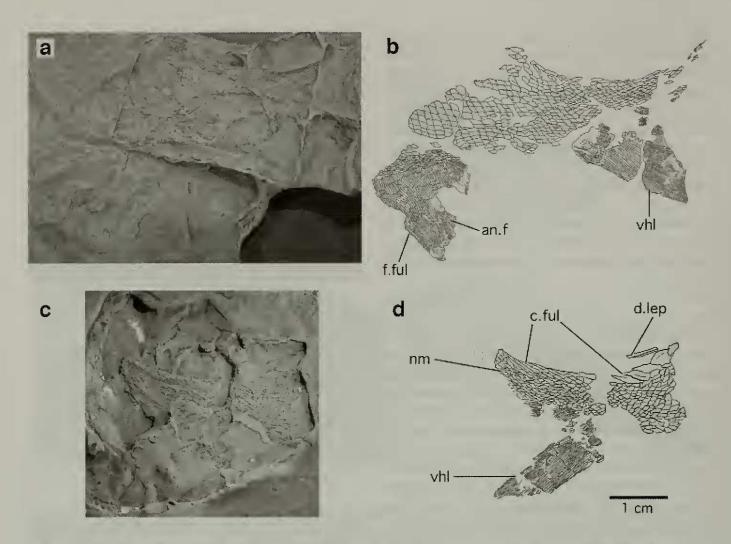


Figure 4. *?Howqualepis youngorum* sp. nov. a. photograph and b. line drawing of the anal and caudal fins of ANU V2929A, c. photograph and d. line drawing of the caudal fin of the holotype counterpart (ANU V2929B).

forwards to above the anal fin (Fig. 4c, d). There are also isolated patches of scales preserved above and to the rear of the pelvic fins (Fig. 3). Very little of the scale ornamentation has been preserved. The visible scale types are described in accordance with the zonation terminology as proposed in in Esin (1990) and employed in Trinajastic (1999).

Area C = flank scales extending from above the pelvic fins to above the anal fin. Scales are elongate and rectangular, with rostrocaudal length being at least twice the height of the scale. Ventral margin is gently convex. The disposition of the peg and socket articulation is unknown in the scales close to the pelvic fins and absent in the scales near the anal fin. Free field ornamentation is poorly preserved but individual scales show remnants of longitudinal furrows. Scales from near the front and rear of the field seem to have two or three serrations protruding along the caudal edge suggesting little or no rostrocaudal decrease in the number of serrations.

Area D = scales anterior to the caudal fin and on the notochordal mass of the caudal fin.

Scales anterior to the caudal fin are rhombic in form, becoming smaller and increasingly elongate on the notochordal mass of the fin. Scales near area C have a gently convex ventral margin, becoming less prominent towards the caudal fin until the margin is completely straight at those scales near the caudal inversion. Peg and socket articulation is absent. The free field is smooth with no preserved traces of raised ornamentation. Posterior serrations range from two in scales near area C to none on those scales on the caudal fin.

Area H = scales adjacent to the base of the anal fin. These scales are small, elongate rhomboids. Peg and socket articulation is not visible and probably absent. There is no evidence of ornamentation or posterior ridges.

The only dermal scutes that have been preserved are an articulated series visible anterior to the dorsal caudal lobe and extending over the dorsal margin of the caudal fin (Fig 3b, c). Anterior to the caudal fin, the scutes are triangular plates with a caudally-

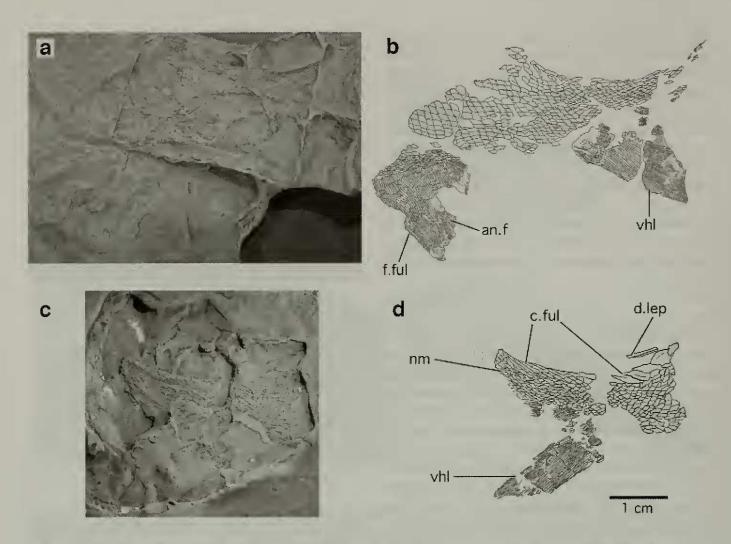


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The only dermal scutes that have been preserved are an articulated series visible anterior to the dorsal caudal lobe and extending over the dorsal margin of the caudal fin (Fig 3b, c). Anterior to the caudal fin, the scutes are triangular plates with a caudallydirected apex and are about three times longer than the adjacent flank scales. As the series progresses posteriorly over the notochordal mass of the caudal fin, the scutes narrow and spine-like with extensive overlap between the individual scutes.

Redescription of the pectoral fin of *Howqualepis* rostridens

Long (1988) described the pectoral fin of *Howqualepis rostridens* as consisting of 25 primary lepidotrichia that are unsegmented for most of their extent, save for some secondary division near the fin margin. A complete pectoral fin was not figured and re-examination of this form has revealed the fin to be more extensive than previously recognised (Fig. 5). Additionally, the leading edge of the pectoral and other fins was described as having short, parallel rays similar to fringing fulcra, but not paired (ibid). A similar condition in *Donnrosenia* led to Long et. al (2008) to diagnose the Howqualepididae as possessing short spine-like lepidotrichia in lieu of true fringing fulcra.

The anterior two-thirds of the fin consist of c.25 lepidotrichia that possess extensive proximally unsegmented sections that in some specimens display distal bifurcation. At the lateral margins, these primary rays branch into a fringe of narrow, segments. The relative length of the proximal rays to the segmented

fringe is variable, with the unsegmented region accounting for between 75-90% of the length of the fin. There appears to be no correlation between the degree of distal segmentation and the size of the specimen.

Posterior of the unsegmented rays are at more than 10 additional primary lepidotrichia that are segmented from base to margin, again displaying a variable degree of distal branching. The pectoral fin of *H. rostridens* was thus broader in shape and less-extensively unsegmented than has previously been described. In the majority of specimens, the delicate elements of the posterior rays and terminal fringe are scattered or missing, leaving only the thick unsegmented proximal sections in articulation. This configuration of the pectoral fin-rays is similar to that of a number of Carboniferous taxa including *Rhadinichthys* (Moy-Thomas & Bradley Dyne, 1938).

On the leading edge of the pectoral fins of *Howqualepis rostridens*, *?H. youngorum* sp.nov and *Donnrosenia*, the terminal sections of the otherwise unsegmented marginal fin rays branch at least twice, to forming narrow spine-like elements that are not obviously paired. These elements are called "terminal lepidotrichia" in *Cheirolepis* (Pearson and Westoll, 1979) and *Melanecta* (Coates, 1998) or "cutwater lepidotrichia" in the Howqualepididae

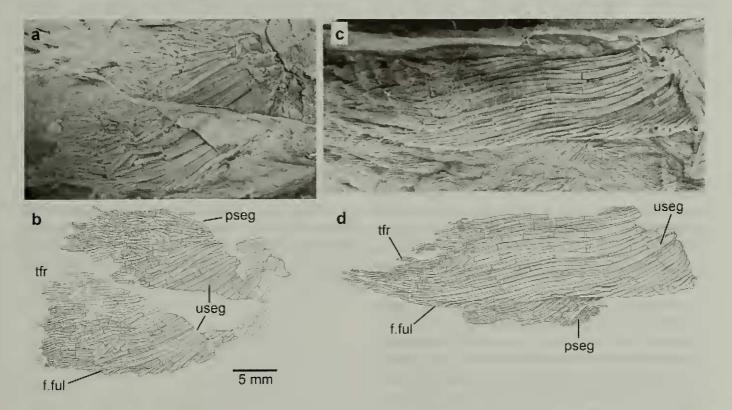


Figure 5. Pectoral fin of *Howqualepis rostridens*. a. photograph and b. line drawing of the fin of MV P.160857. c. photograph and d. line drawing of the fin of MV P.160851B. In this specimen, the posterior section has partially torn off and folded to be visible ventral of the anterior edge of the fin.

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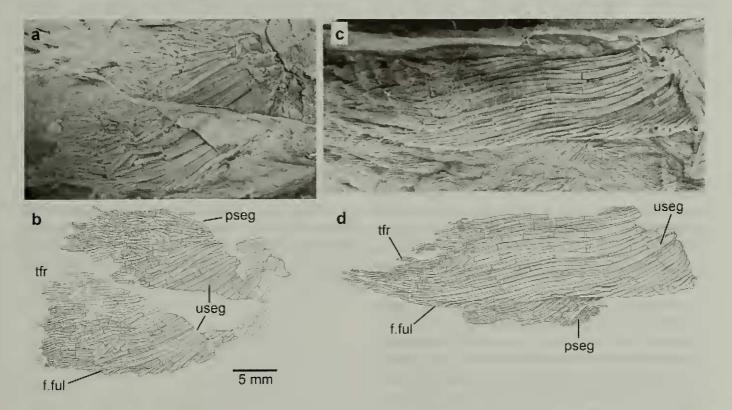


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(Long, Choo and Young, 2008). In a recent study, such structures fall into Arratia's "Pattern A" class of fringing fulcra, formed from overlapping branched projections of the anteriormost lepidotrichia (Arratia, in press), a condition found in all undisputed Devonian actinopterygians with the exception of Tegeolepis which appears to lack any sort of spiny cutwater (Dunkle and Schaeffer, 1973). The fulcra of Cheirolepis, which are of similar form to those of the Howqualepididae, comprise distally enlarged hemilepidotrichia that partially enclose their paired counterparts (Arratia, in press). The more obviously paired structures present in Moythomasia and "Mimia" (also falling within "Pattern A") are the result of the terminal segments being of equal length and in medial contact. Given that the scheme proposed by Arratia (and adopted here) means that all Devonian fringing fulcra are in fact modified spinelike lepidotrichia (merely differing in the nature of contact between the hemilepidotrichia), the diagnosis of Howqualepidiae has been adjusted accordingly in the systematic description.

DISCUSSION

Long, Choo and Young (2008) erected the Howqualepididae, comprising Howqualepis rostridens from Mount Howitt, Victoria and Donnrosenia schaefferi from the Aztec Siltstone of Antarctica. ANU V2929 appears to represent a third taxon within this clade (Fig. 6). All three fish have an elongate body form with macromeric squamation; long-based pelvic fins; small fringing fulcra without medial contact between the distal hemilepidotrichia, and extensive unsegmented primary lepidotrichia that comprise most of the length of the pectoral fin. Among the other Devonian actinopterygians, only Tegeolepis clarki (Dunkle and Schaeffer, 1973) possesses extensive unsegmented pectoral lepidotrichia but is distinguished from the Gondwanan forms in lacking a terminal segmented fringe on the pectoral fins, in possessing micromeric squamation and having small, short-based pelvic fins.

Assigning the Bunga Bed taxon to a genus is rendered difficult owing to the lack of key skull characters that are used to characterise *Howqualepis rostridens* from the similar *Donnrosenia*. For example, *H. rostridens* possesses an extremely long maxillary blade, a dentigerous rostral and small, dorsoventrally compressed premaxillae (Long 1988). *Donnrosenia* displays a short, deep maxillary blade, dorsoventrally prominent premaxillae, a small accessory operculum and much smaller teeth than *Howqualepis* (Long, Choo and Young, 2008).

ANU V2929 is considered to be closer *H.rostridens* in having more extensive unsegmented pectoral lepidotrichia and relatively smaller scales than *Donnrosenia*. The pectoral fins of ANU V2929 are more similar to that of *H. rostridens* in that both forms possess unsegmented lepidotrichia that account for over 75% of the maximum length of the fin. Those of *Donnrosenia* account for less than 70% of the maximum fin length (Long, Choo and Young, 2008. Fig.7).

Based on these anatomical similarities and pending the discovery of skull material for this taxon, ANU V2929 is tentatively assigned to *Howqualepis*. The Bunga Bed form is not conspecific with *H*. *rostridens* and is distinguished in having a larger anal fin with a greater number of primary lepidotrichia and in possessing porous dermal ornamentation of the pectoral girdle.

The presence of a grade of Devonian actinopterygian so far found exclusively in Middle Devonian freshwater deposits of southeastern Australia and Victoria Land, Antarctica highlights the close biogeographical similarity between the fossil faunas of these two regions. The apparent absence of these ray-finned fishes in Devonian sites outside this area also adds to a growing body of fossil evidence that indicates a regionally endemic freshwater vertebrate fauna within Middle Devonian Eastern Gondwana. Similarities in key taxa of placoderms (Young 1988, Young and Long 2005), acanthodians (Long 1983, Young 1989, Young & Burrow 2004), chondrichthyans (Young 1982, 2007; Long & Young 1995) and dipnoans (Long 1992, 2003) have been well documented.

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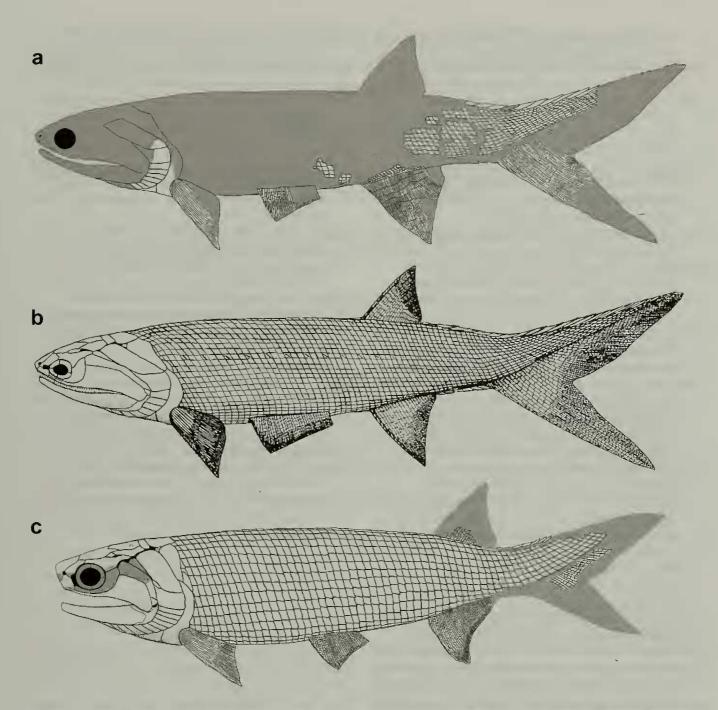


Figure 6. Comparison of the three known species of the Howqualepididae. Reconstructions presented in lateral view and are not to scale. Unknown parts of the anatomy are represented by dark grey areas. a. *?Howqualepis youngorum* sp.nov., based on the preserved extent of the holotype with outline based on *H. rostridens*, c.14cm long. b. *Howqualepis rostridens* from Mount Howitt, Victoria (modified after Long, 1988). Size of specimens range from 20-50cm. c. *Donnrosenia schaefferi* from the Aztec Siltstone, Southern Victoria Land, Antarctica (from Long et.al, 2008), c. 14cm long.

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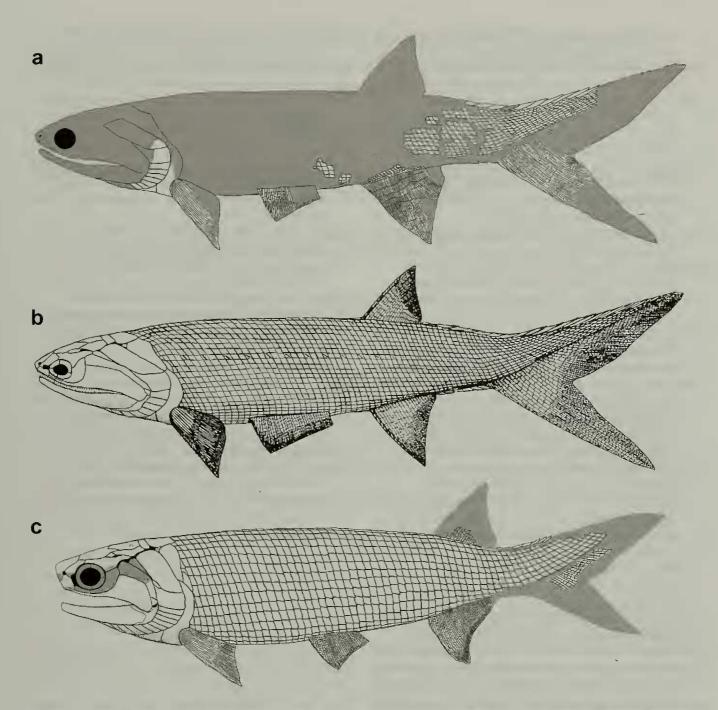


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